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WHAT IS FLOWER

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Secret of success of flowering plants is the presence of well developed sexual reproductive organs in the form of flower and mechanism of cross-pollination. Their sudden appearance in Cretaceous rapid evolution and diversification in short period is puzzling. A large population of early angiosperms has become extinct and many modern species having disappeared more or less completely from their original home land , have occupied large tracts of altogether new areas. Charles Darwin (1959) commented that development and evolution of flowering plants is "An abominable Mystery" This phrase has become a symbol of a key gap in our understanding of plant evolution. Various problems related to flowers are, how ancient flower is; what is its cradle home; how an ancient flower looks like; who are their immediate ancestors; what is the morphological nature of flower and its organs; nature and morphology of placentation; evocation of flower and evolution of flower from simple to complex flower, etc. Answer to all these questions are searched in studying the comparative morphology, fossil records, cladistic studies with the aid of computation and molecular analysis of living plants. The discovery of fossil flower *Archaefructus lianingensis (*Sun *et al.* 1998) from Jixin province of North- East China belonging to Jurassic or early Cretaceous strata, estimated about 145 million years old has solved the problems to some extent. This flower is so far the oldest discovered fossil remain and it resembles the primitive extant flower of *Magnolia.* Recently established family Hydatellaceae is considered the most primitive family of angiosperms and its genus *Trithuria* is closely related to *Archaefractus.*

Regarding the cradle home of flowering plants evidences are more in favor of their origin from South-East-Asia-Australia. However Sun *et al.*(1998) proposed that North-East China can also be the center of origin because of the discovery of *Archaefructus* from this region.

Ancestors of flowering plants have been looked into various plant groups of pteridophytes and gymnosperms. Cladistic studies and molecular analysis of nuclear, plastidal and mitochondrial genomes have revealed that members of Gnetales are closest living relatives of primitive living angiosperms and their phylogeny is rooted through families like *Amborella,* Nymphaeaceae, Illiciales, Trimeniaceae and Austrobailayaceae (ANITA) and genera *Trithuria* and *Ceratophyllum* are close to *Archaefructus.*

Goethe (1790) stated that, "the flower is a metamorphosed shoot and later DeCandolle (1827) laid the foundation of classical concept of flower morphology and stated that flower is a condensed shoot and floral organs are morphologically foliar in nature. Although, later many other concepts came but the classical concept is strongly supported by most of the workers on the basis of evidences collected from comparative morphology, teratological studies and vascular supply of the flower. The carpels are either conduplicate folded or induplicate folded. In *Ochna multiflora* having a multicarpellary and syncarpus ovary the carpels are conduplicately folded (Govil and Kumar, 2010). Which placentation, axile or parietal is primitive was question marked by Puri (1952), however Saxena and Govil (1995) proposed that parietal placentation is primitive and axile is advanced. To facilitate cross-pollination there is a co-evolution of flower from simple to complex flowers and biotic pollinators. Genes have been identified for the expression of different floral organs. Many more mysteries of flower will be solved as more and more data is collected on fossils and molecular analysis of primitive flowering plants.

Key words: Flower, origin, evolution, morphology, evocation

On the outset I wish to thank the members of the executive members of the society and the members for electing and honoring me with this post of President of the society, I feel highly honored. I am fully conscious of my limitations and responsibilities attached to this office, especially, when I know that all my predecessors who occupied this position were eminent scholars. On this occasion I remember my revered teachers late Professor V. Puri and late

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Professor Y.S. Murty who initiated and guided me to the glorious path of studies on flower morphology. I am indeed grateful to them for their kindness and blessings which I cherished always.

I have chosen this topic **What is Flower** because of many reasons; firstly, this month we are celebrating the 150th year of publication of Origin of Species, 200th birth day of Charles Darwin, and100th birth day of Professor V. Puri, a well known floral morphologist and evolutionist.

We respond so differently to the charm of flower- a poet describes a flower in his poetic language and a student of botany, who studies it in much greater details, finds so much difference of opinion as to its morphology. Flower morphology is considered to be the most important part from systematic and evolutionary points of views.

Goethe (1749-1832) a poet, thinker and philosopher explained the morphology and philosophy of the flower in a metaphoric language that flower is a result of metamorphosis of vegetative bud, and floral organs are equivalent to foliage leaves.

This was later elaborated by De Candolle (1827) who put forward the **Classical concept of floral morphology.**

Puri (1951) supported the classical concept of De Candolle (1827) based on the evidences gathered from comparative morphology, ontogeny and floral vasculature. He was a strong exponent of classical concept and in support of this he and his students studied a number of species from different families (Govil 1995).

After Darwin (1859) made the statement that development and evolution of flowering plants is an "**abominable mystery**" a number of phylogenists and evolutionists got attracted to the problem of origin and evolution of flower. A sudden spread of flowering plants in middle of Cretaceous was a violent expansion of these plants due to natural and geographical events of great magnitude, which led to great diversified plasticity in these plants. The events included vibratory movement of the earth's crust, leading to great mountain building, climatic changes, and Gondwana break up .To resolve this problem palaeobotanists had much to offer in the solution of various mysteries related to flower, because the past history of ancient flower is buried in the Earth crust in the form of fossils. Many questions have been raised regarding flower by the morphologists, some of them are:

1. How ancient a flower is?
2. Where did they originate?
3. How did an ancient flower look like?
4. Were they monophyletic or polyphyletic in origin?
5. Who were their immediate ancestors?
6. How flower evocation takes place?
7. What is its morphological nature?

Ever since Darwin (1859) mentioned that evolution of flowering plants is an abominable mystery, these questions puzzled the plant morphologists and many explanations have come from them to resolve these problems. Most of the explanations are based on the data available from comparative morphology, fossil records and cladistic studies. Floral morphology is explained on the basis of floral vasculature. Recent techniques of molecular analysis and gene identification have also helped in explaining the above questions.

Origin of flower

Origin of flower has remained one of the most popular discussion topics in the history of evolutionary biology. It is directly related to the origin of flowering plants. Study of fossils of micro and macro floral organs is the basis of determining the age of flower. Unfortunately our fossil record is scanty as the floral organs are delicate and do not fossilize easily as compared to other organs like stems, leaves, pollen and seed. We have sufficient evidence to assign them to Cretaceous period, but several authors have made claim of their existence in pre-cretaceous period on the basis of discoveries of several micro and macro fossils of pollen, leaves and woods. On further analysis of characters of these fossils, non of these reports is accepted as conclusive evidence of the appearance of a flowering plant before Cretaceous, as many of these fossils of pollen, leaves and woods form some apparent angiospermic characters but none of them had definite features of flowering plants beyond doubt.

Micro- fossils: Pollen or spore remains of *Tetraporina, Triporina, Zonotetraporina* and *Azonotetraporina* of Carboniferous of Palaeozoic described by Naumova(1950) and Tetrzuk (1956,1958) were compared to present day angiospermous pollen like those of *Ulnus* and *Myriophyllum*, however detailed investigations revealed that they are in fact the spores of algae and ferns and not of angiosperms (Scott *et al.* 1960). Similarly pollen remains described from Scotland Coal mines of Jurassic (Mesozoic) by Simpson (1937), which were of two types, monocolpate like those of lilies and tricolpate like those of lotus. Since tricolpate pollen are derived from monocolpate pollen the discovery of tricolpate pollen in Jurassic was considered to be the evidence of existence of angiosperms in that period, but pollen were also found to be of gymnosperms by Hughes and Couper (1958). Similarly, other pollen fossils described from Jurassic were either wrongly interpreted or identified.

The earliest pollen fossils with undisputed angiospermic affinities have been reported from Berremian formations of Cretaceous by a number of workers from different part of the world (Couper 1958, Kemp 1968, Doyle 1969, Doyle *et al*. 1977,). *Clavatipollenites*, an earliest Cretaceous pollen fossil with angiospermous characters having tectate reticulate ornamentation resemble the pollen of members of living Laurales. Doyle *et al*. (1977) stated that in Cretaceous there has been a great divergence and frequency of pollen grains and the occurrence of flowering pollen in late Albian period shows that the flower originated in early Cretaceous.

Macro-fossils: Regarding macro-fossils in the form of leaves and stem remains recorded from Paleozoic and Mesozoic do not throw sufficient light on pre-Cretaceous origin of flowering plants. Presence of reticulate venation in leaf fossils is considered as the evidence for their early existence by many authors. Triassic leaf fossils, namely, *Sanmiguelia* (Brown 1956) a palm like leaf, *Furcula* (Harris 1932) a dicotyledenous type of leaf, *Marcouia* a pinnate leaf, *Pannaulica* with reticulate venation etc. do not support the existence of flower in pre-Cretaceous period as reticulate venation is also found in some gymnosperms and ferns. Further there are no structural details in support of their angiospermic affinities. On similar bases, leaf fossils of Jurassic origin *like Sassendrofilis* (Kuhn1955), grasses (Reissenger1952), *Propalmophyllum* and *Phyllites* (Seward1904) and many other leaf impressions do not support the Mesozoic existence of flowering plants.

Several wood fossils assigned to pre-Cretaceous period like *Suevioxylon zonatum* (Krausel 1928), *Homoxyloxylon rajmahalensis* (Sahni 1932) and species of *Homoxylon* and suggested their affinities with flowering plants were later found to belong to stems of Bennettitales (Bose and Saha 1954) and therefore do not support the origin of flower in pre Cretaceous.

Thus the pre- Cretaceous fossil records so far do not lead us to conclude that flower originated earlier in Paleozoic or Mesozoic and the origin and early evolution of flower remain

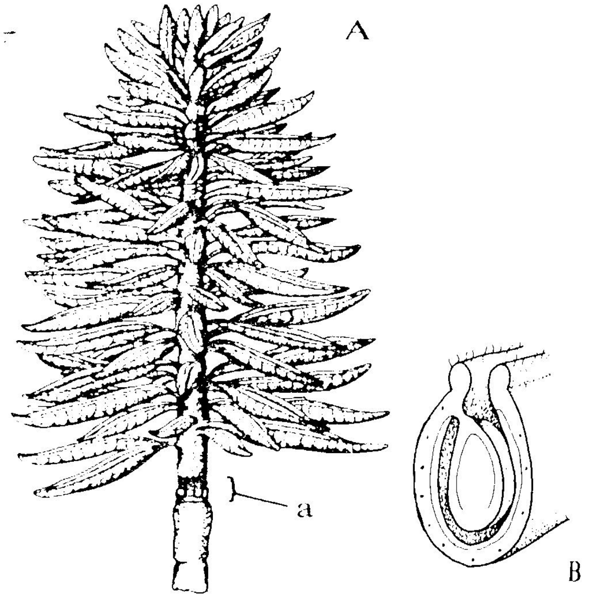

Figure-1 Reconstruction of flower *Archaeanthus* from late Cretaceous Cenomanian of Kansas (Dilcher and Crane 1984) A-follicles B-ovule attached on the margin.

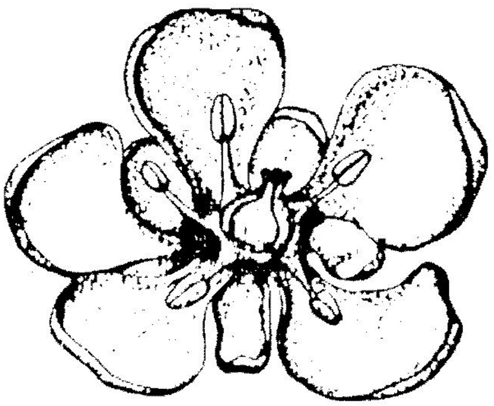

Figure-3 Reconstruction of primitive flower of Mid-Cretaceous (Stewart 1983)

a long standing problem as described by Darwin (1859). However, there are definite evidences based on fossil records that they existed in Cretaceous period.

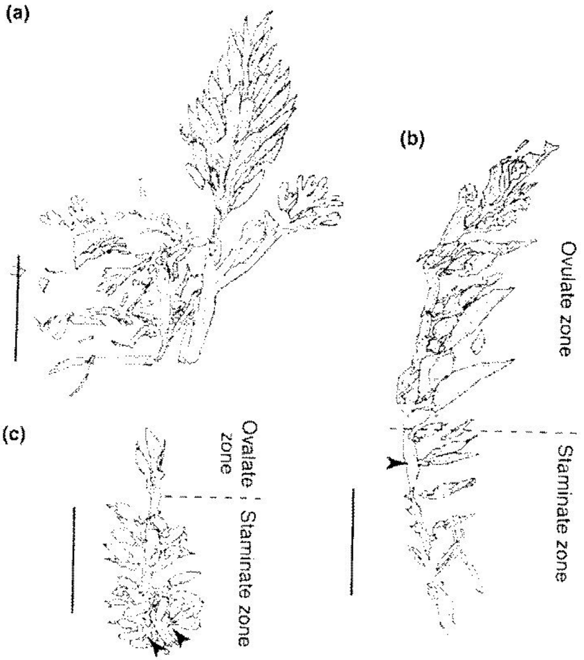

Figure-2 Reconstruction of fructificationof *Archaefructus lianingensis(* Sun e*t al* 2002).

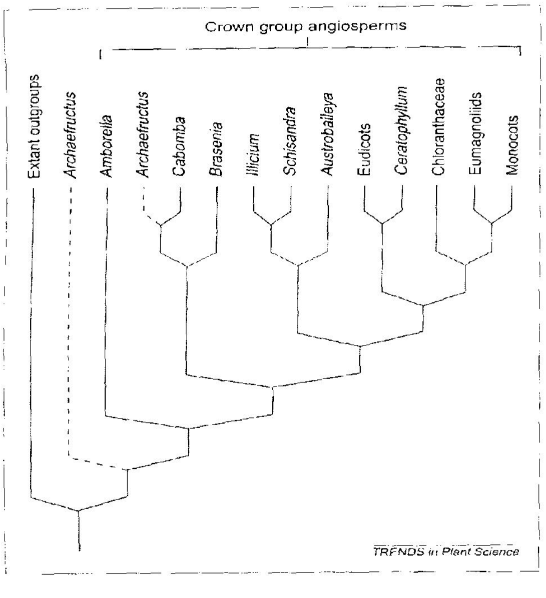

Figure 4: Cladogram of Sun *et al.* (1998) simplified with calomba added, showing two equally parsimonious positions for *Archaefructus* after scorring angiospermous out groups as un-known (inapplicables) for perianthy.

In Cretaceous, a large number of flowering plant fossils have been discovered from Potamac-Group in Virginia (Doyle and Hickey 1976). It appears that there was a sudden appearance of flowering plants in Cretaceous. According to Pacltova (1976), in Cretaceous flowering plants showed rapid evolution of many species in short duration, but most of these species became extinct giving rise to tertiary ones. According to her there are many authenticated reports to the effect that a very large population of early angiosperms have become extinct and many modern species having disappeared completely from their original home-land and have occupied large areas of altogether new.

Basinger and Dilcher (1980) reconstructed a pentamerous flower from the remains of early late Cretaceous. Later Dilcher and Crane (1984) described an angiospermic flower from Cenomanian of Kansas and named it *Archaeanthus* (Fig.1). In their reconstruction the flower has 100-130 follicles, spirally arranged and each follicle has 10-18 seeds. According to them this flower resembles the flower of Magnolidae. Friis *et al.*(1994) also recovered remains of flower organs from Cretaceous formations, but all these assemblages are poorly preserved and morphologically possess disorganized patterns. The ancestry of these fossil flowers is estimated to about 131-124 million year old belonging to Hauterivian formation.

Archaefructus lianingensis: Sun *et al.* (1998) discovered a beautiful specimen of flower fossil from Jixi Province of North-East China, a site of western Lianing, and named it *Archaefructus lianingensis*(Fig.2). This fossil flower estimated to belong to Jurassic or Early Cretaceous strata dating 145 million year old. The specimen has a leaf like structure attached to an axis terminating into about 48 follicular fruits and below this there are scars of stamens attachment. She described it as a primitive form of flower with distinct features of primitiveness in the early history of flower evolution. This flower fossil morphologically resembles extant angiosperm flower of *Magnolia* and fossil flower of *Archeanthus* (Dilcher and Crane 1984) dating 95 million year old. In both *Archaeanthus* and *Archaefructus* the pad shaped follicle fruits have conduplicate carpels as is found in flowers of present day primitive families. Thus so far with convincing evidences the earliest flower is about 145 million year old belonging to early Cretaceous.

Cradle home of early flowering plants

There are different views as to the place of their origin on earth. During the past century an accepted view was that the flowering plants had originated in all regions of North Hemisphere, from Arctic to Tropic. Seward (1926, 1933) considered on the basis of fossils discovered of leaves and inflorescence of *Artocarpus* from Lower Cretaceous in Greenland in Arctic. He believed that during that period the climate of this region was warm. On the other hand Krassilov (1982) and Vakhrameev (1978 and 1991) suggested that Atlantic coasts, central Asia and Mongolia are the fountain head of flowering plants. Most of the scientists, however believe that flowering plants originated in tropical regions and spread towards polar areas during the course of rapid diversification. According to this view the area which has the largest number of so called primitive living flowering plants and also the center of diversity *i.e.* where large number of species exist, is the cradle home of flowering plants. In support of this view Smith (1972) identified 39 families with 490 genera and over 12,200 species as the most primitive and of these 34 families are represented in South-East Asia through Malaya into Eastern Australia, 17 of these occur in tropical Africa and Madagascar and 18 in tropical America. On the basis of this analysis Smith (1972) postulated that flowering plants originated in the area of South-Eastern Asiatic- Indo-Malaysian tropics where from they migrated to other parts of the world. Although, ecological and physico-geographical conditions were not stable in South- East-Asia and Australia than in tropical America or tropical Africa, yet they sustained the most primitive in this region and hence this can be the cradle home of flowering plants. Interestingly, America and tropical Africa are extremely rich in flora but they are poorer in primitive flora (Takhtajan 1969). He argued that some primitive families like Magnoliaceae, Winteraceae, Himentenderaceae and Degeneriaceae must have existed there previously, then some of the representatives of these families must have survived and rest became extinct. This hypothesis of Takhtajan (1969) has been questioned and argued whether the center of distribution can essentially be the place of origin also, because this region still retains some isolated and distinct population of plant which has exceedingly large number of primitive characters. A region that allowed retention of so many primitive characters can not obviously be the place of origin of earliest flowering plants, because the two situations require two different sets of environment. The origin of new species is possible under more challenging conditions of environment while the tropical rain forest provide more congenial and equitable conditions of plenty of rainfall and sun light. Takhtajan (1976) proposed the area between Assam and Fiji show isolated primitive type of closely related families and genera. On the other hand Guedge (1979) and Puri (1980) believed that rain forest contain complete spectrum of primitive and advanced families. Stebbins (1974) suggested that tropical rain forest is the asylum into which freshly produced flowering plants some how migrated and have since been preserved in more or less unchanged make up.

Axelrod (1959, 1970) and Brenner (1996) believed that Gondwanaland is the cradle home of flowering plants, because the tropical upland of Gondwanaland with seasonal droughts in early Mesozoic world would have been the best suited place for flowering plants to grow. After the discovery of *Archaefructus* an earliest fossil flower in China Sun *et al.* (1998) that the Eastern China is he dawning site or one of the site of origin of flowering plants. She remarked that "progress in the study of the dawning process of flower has always been in study and the discovery of *Archaefructus* is only the first step in demystifying the "*abominable mystery*" put by Darwin (1859) on the early evolution of flowering plants.

What was the shape of ancient flower

What was the morphology of extinct flower from which the present day flower evolved? Arber and Parkin (1907,1908) on the basis of comparative morphology and of course much on speculation reconstructed a hypothetical group named "Hemiangiosperms" with hypothetical flower in which perianths, microsporophylls and megasporophylls are represented as supposed to be in primitive flower. Their reconstruction was based on the bisexual "flower" of Cycadeoidea of Cycadeoidales an extinct gymnosperm. Another reconstruction was given by Corner (1949) in which an ancient angiosperm flower was shown with terminal flower having arillate seed bearing fruits. Sun *et al.* (1998) proposed that *Archaefrutus* flower shows some likeness with the living flower of *Magnolia.* Earlier Cornet (1980) on the basis of *Sammiguelia* and Dilcher and Crane (1984) on the basis of *Archaeanthus* also reconstructed ancient flower similar to flower of Chloranthaceae and *Magnolia* respectively (Fig.3). Crane (1995) compared the ancient flower with the flower of *Sarcandra glabra.*

Who were the immediate ancestors of flower

Immediate ancestors of flower are searched amongst the members of pteridophytes and gymnosperms. Some of the theories suggested are, 1. Isoetes-Monocotyledons theory (Campbell 1828), Eusporangiate-fern theory (Eames 1961), Caytoniales theory (Thomas (1925), Pteridosperm theory (Andrews 1961), Cycadeoidalean theory (Bessey 1897, Hallier1908, Arber and Parkin 1907), Coniferale- Amentiferae theory , (Eichler1875-1878, Hagerup 1934-1936), Gnetalian-Angiosperm theory (Engler and Gilg 1924,Crane 1985) etc. All these authors found characters of reproductive organs of these groups comparable to angiosperm flower, but in all cases the resemblances are apparent and none of these theories has solved the mystery of ancestry of flower. According to Pant (1971) the evidences from comparative morphology are unreliable and fail to draw any conclusion.

In recent years several studies have been made to link theories using cladistic approach and molecular analysis, but there is no general agreement that any of these taxa are related to angiosperms (Bateman *et al.* 2006, Doyle 2006, Friis *et al.* 2007, Frohlich and Chan 2007).

Phylogeny of flowering plants

A huge amount of data of morphological and molecular characters has been analyzed through computer using soft-wares. Cladistic analysis has revealed that there is a direct link between angiosperms and Gnetales (Crane 1985a, b), while Doyle and Donoghue (1992) traced angiosperms basal in anthophyte-*Caytonia*, Glossopterids and Corystosperms in one clad They also suggested that flower in angiosperms Bennittitales and Gnetales originated independently. Doyle (1994) and Rothwell and Sorbet (1994) proposed another clad with link between Coniferophytes, Gnetales and angiosperms. According to Doyle (1994) the flower of Gnetales are more primitive and are derived from coniferous cones and angiosperm flowers are derived by elaboration and aggregation of parts.

A new twist to the problem of phylogeny of flower arose with the discovery of *Archaefructus* from early Cretaceous period. Many extant flowers and fossil flowers show simple flowers in primitive families of angiosperms-like Chloranthaceae, *Ceratophyllum*, *Hydatellacea* and *Archaefructus* fossil flower. Endress and Doyle (2009) evaluated early floral evaluation in angiosperms by parsimony optimization of morphological characters on phylogenetic trees derived from morphological and molecular data (Fig.4). According to them flower of these families are reduced rather than primitively simple. Donoghue and Doyle (2000), Burleigh and Mathews (2004), Soltis *et al.* (2005) remarked that molecular analyses contradict one of the few points on which morphological analyses agreed that Gnetales are closest living relatives of the angiosperms. Doyle (2008) based on molecular analyses suggested that Gnetales have relationship with conifers rather than angiosperms.

The molecular analyses of basal groups of angiosperms established that families, *Amborella*, Nymphaeales, Illiciales, Trimenicaceae and Austrobaileyales (ANITA) form basal core to most of the angiosperms and termed them “Mesoangiospermae” (Cantino *et al.* 2007). The analyses of mitochondrial genes showed that *Amborella* and Nymphaeales form a clad (Barkman *et al.* 2000) and the plastid genome support that they form successive branches (Jansen *et al.* 2007 and Moore *et al.* 2007).

After the discovery of fossil flowers from Lower Cretaceous namely *Archaeanthus and establishment of “**core angiosperms**”* based on the computation of morphological and molecular data we have reached to the conclusion that so far the earliest flower existed in Lower Cretaceous and at that time angiosperms were dominating. Some of the present day members of angiosperms with simple flowers like those of *Archaefructus* and other similar flowers may be the ancestors. However, the origin and phylogeny of flower will remain for ever one of the most popular topics of discussion in evolutionary biology.

Another problem related to phylogeny of flowering plants is whether they are polyphyletic or monophyletic in origin. Those who believe in polyphyletic origin they argue that because of the diverse structure of flowers there may be more than one primitive flower existed which gave rise to present day flower (Hagerup 1934, Hughes 1976, Sun *et al.*1998). Probably three Mesozoicgroups, Caytoniales, Czekanowskiales and Dirhopalostachyaceae are the major source of angiosperm characters and considered them as “Proangiosperms” (Krassilov1982). However, Doyle *et al.* (1977) doubted the existence of any of the Proangiosperms in Jurassic of Mesozoic. Monophyletic origin is supported on the basis of the consistency in many characters such as, life history, embryo structure, double fertilization, triple fusion, presence of endosperm and embryogenesis, etc. (Schnarf 1936, Parkin 1957). Based on DNA sequencing of five mitochondrial, plastid and nuclear genes from all the angiosperms and gymnosperms (105 species. 103 genera and 63 families) it was concluded that *Amborella* a is the sister of all the angiosperms and is basal in position forming a monophyletic group with Nymphales, Illiciales Trimeniaceae and *Austrobaileya* (ANITA) in angiosperms (Qui *et al.* 1999). This does not support the Anthophytic hypothesis of Crane *et al.* (1995).

DNA sequencing of plastid gene Cox1 18s, DNA rbe1 also supports the hypothesis that there is a link between Gnetales and angiosperms (Bowe *et al.* 1997, Chaw *et al.*2005, Doyle *et al.* 1994). Nixon *et al.* (1994) held the view that Gnetales are the paraphyletic group. However, Doyle (1998) believed that molecular studies do resolve some of the Phylogenetic problems but at the same time introduce some new issues, since molecular analysis does not take into account the fossils which are essential in order to formulate any hypothesis on the origin of flower.

Evocation of flower

Most unanswered question in the developmental biology is that what prompts the vegetative shoot to transit into a reproductive phase. On the basis of anatomical, morphological and physiological studies one thing is clear that flowering is not an abrupt or spontaneous developmental decision of the plant, rather it is the culmination of closely integrated programmed physiological and developmental changes which evocate flowering. In the process of flowering the most critical aspect is the floral initiation involving differentiation of floral primordial that alone marks the transition from vegetative to reproductive phase.

In the study of floral evocation many question are under consideration such as 1,.how apical meristem become determined to produce floral primordial, 2,. factors that establish floral meristem identity 3,what are the signals that evoke transition from vegetative to reproductive stage 4 how do these signals function 5,what are the genes involved in flower evocation if at all. Multifactorial control of environment, endogenous signals and hormones are involved in whole of the process (Bernier 1988, Mc Daniel *et al.* 1992).

According to multifactorial model the flower evocation is controlled by a number of promoters and inhibitors, including phytohormones and assimilates. Flowering can occur only when the limiting factors are present at the apex in the appropriate concentrations and at the right time. Different factors could be limiting for flowering in different genetic sets under particular environmental conditions. Genetic analysis of flowering time in pea, cereals, and *Arabidopsis* whose multiple genes that control flowering time have been identified, some of these genes promote flowering and some repress it, some interact with environmental variables and other appear to act autonomously (Koorneepfetal *et al.*1998).

The development of an organ is under a set of genes called homeotic genes and the transformation of an organ into another organ under the control of homeotic genes is known as homeosis, such type of mutation are termed as homeosis or homeotic mutation. Baur (1924) in *Antirrhinum* and Laibach (1943) in *Arabidopsis* were the first to report various types of homeotic and other types of transformation, and the first report of isolation of homeotic gene *DEFICIENS* (*DEF*) was made by Sommer *et al.* (1990) in *Antirrhinum* and *AGAMOUS* (*AG*) by Yanofsky *et al.* (1990) in *Arabidopsis*. Now

Arabidopsis thaliana is extensively used as a model organism for elucidating the process of flowering by a number of workers. Gene *DEF* and *AGAMOUS* code for a transcription of factor protein that apparently control the expression of many other genes and this protein showed similarities to certain transcription factors isolated earlier in yeast and humans This master gene was designated as MADS-Box which is an acronym of yeast *MCM1* gene of the mating type locus, A and D from *AGAMOUS* gene of *Arobidopsis*- D from *DEFICIENS* of *Antirrhinum* and S from the serum of response factor known in human and serving as a transcription factor (Schwarz-Sommer *et al.* 1990). Much of our knowledge about the homeotic genes cloned and which are involved in the development of flower in *Arabidopsis thaliana* is due to the work done by Meyerowitz (1994), Yanofsky *et al.* (1990) and Weigel (1997,1998). They have analyzed and cloned gene involved for the development of different organs. These genes are termed as follows-

1. Floral meristem identifying genes (*LEAFY1, APETALA1, CAULIFLOWER*1).
2. Floral meristem structuring genes *CLA VAT A1, CLA VAT A3 PERIANTH*).
3. Organ identifying genes (*APT ALA1, APETALA2, APETALA3 PISTILLATA* and *AGAMOUS).*
4. Cadastral gene (*SUPERMAN, LEUNIG*).

Floral meristem structuring genes determine the site and number of floral organ primordial that will develop in each whorl, subsequently this pattern of organ primordia is elaborated by the organ identifying and cadastral genes. The organ identifying homeotic genes are expressed each in two neighboring whorls and through their interaction ultimately determine the organ type. Coen and Meyerowitz (1991) developed a comprehensive model to explain the flower development which is known as ABC model.

This model is applicable in both *Antirrhinum* and *Arabidopsis*. The cadastral genes restrict the expression of the organ identity genes to specific regions of the floral meristem. Mutation in the cadastral gene (*SUPERMAN SUP*) result in the development of extra stamens at the expense of the carpels (Schultz *et al.* 1991, Bowman1997). ABC model holds that organ identity is established overlapping functions of three classes of homeotic genes, the combination of these gene classes result in specific organ identity.

1. If class A gene is expressed, then sepals develop.
2. If class A and B genes expressed then petal develop.
3. If class B and C gene expressed then stamens develop.
4. If class C gene expressed alone then carpels developed.

This model also implies that there must be mechanism to inhibit gene expression Class A gene can only be expressed in the outer two whorls not in the inner two whorls. Conversely Class C genes can only be expressed in the inner two whorls and not in the out two whorls. Class A genes inhibit the expression of class C gene and vice-versa. Similarly some thing must prevent the expression of class B genes in the inner most whorl. In *Arabidopsis thaliana* the key regulatory genes that act in each three classes are as follows

A- Group genes are *APETALA* 1 (*AP* 1) and *APETALA* 2 (*AP* 2).
B- Group genes are *PISTILATA (PL*) and *APETALA 3 (AP 3*).
C- Group genes are *AGAMOUS* (AG).

Their mutants exhibit homeotic phenotype each displaying a transformation of floral organ identity in two adjacent whorls. In mutants in group B genes for instance petal are transformed into sepals and stamens into carpels. Similarly a plant carries a mutation in *AGAMOUS* gene, then there is no class C activity and class A activity spreads into the inner two whorls *i.e* .the resulting flower consists of whorls with sepals, petals, petals and sepals.

Although, ABC model with three classes of genes is a good working model in understanding control of flower development, but recent discoveries in last few years have shown that there must be some other gene or genes involved in flower development. A new set of genes called *SEP ATLA T A* (SEP) genes or class D genes have been included. Kramer *et al.* (2003) have shown gene duplication and protein dimerization have played a role in the evolution of floral types as exemplified by their studies in Ranunculaceae.

Morphology of flower

As mentioned earlier, Goethe (1790) explained the morphology or philosophy of flower and his interpretation is regarded the classical interpretation. According to him, flower is a modification of a vegetative bud in which the nodes have condensed and the individual floral organs are equivalent to leaf, but not modified leaves. Similarity in morphology and anatomy of the flower are satisfactorily explained in this concept. Although many authors agree that sepals are equivalent to foliage leaves but opinion differ with regards to stamens and carpels. Petals are usually believed to be the products of sterilization of stamens. The foliar nature of stamens is well indicated in members of primitive families of Ranales and Magnoliales and their evolution from foliar to terete type is well documented. The fact that petals are sterilized stamens is shown in *Eupomatia bennettii*, in which stamens develop centripetally in many whorls and petals form a whorl in between replacing stamen whorl.

Histological studies of the floral bud and vegetative apex seem to indicate that the floral apex is just an ontogenetic modification of the vegetative apex. Differences between them are believed to be associated with the mode of growth exhibited by them. The transformation of vegetative apex into floral apex is also under the control of homeotic genes which function under a set of multifactorial factors.

Amongst the floral organs carpel is the most complicated and controversial organ and has attracted the attention of many morphologists so much so that it is considered synonymous with flower. There are two main schools of thoughts (i) Classical concept and (ii) Neo-morphological concept. According to classical concept carpel is morphologically similar to fertile leaves bearing ovules attached to their margins. Puri (1951 and 1960 considered that in ovary, carpel margins are involutely folded adaxially and inwardly as supported by morphology and vascular supply. In his support he has cited many examples from a number of species belonging to different families. On the other hand Swamy and Periasamy (1964) considered that the carpel margins are conduplicately folded adaxially as observed in the ontogeny of primitive flowers of primitive families. In involute folding of carpel according to Puri (1960) the ovules are attached on the margins of the carpel while according to Swamy (1956) they are attached on the adaxial surface. The conduplicate carpels are present in primitive monocarpellary or apocarpous ovaries and involute carpels in multicarpellary syncarpous ovaries of advanced families. Our recent studies on *Ochna multiflora* of Ochnaceae reveal that its flowers are multicarpellary syncarpous but carpels show conduplicate folding and ovules are axial in position as revealed by floral anatomy and vascular supply to carpels. Since *Ochna* belongs to primitive family with multicarpellary syncarpous condition, the presence of conduplicate folding is a peculiar condition. In *Ochna* the style is gynobasic and fruits are nutlets which separate out before fertilization, probably the presence of condupicate condition may be intermediate condition in the process of transition from conduplicate to involute folding.

The profounder of new morphology offers a highly speculative, historical or phylogenetic interpretation. According to Meeuse (1975) the ovary is an out growth from the base of a branch system bearing ovule. He considered ovary as a "spurious floral apex" which means that the floral apex is actually a fusion product of so many gonoclads bearing ovules. Melville (1962, 1968) a neo-morphologist considered the gonophyll to be the basic unit of floral construction. It is a composite organ consisting of a leaf and a branch. In the reproductive phase only the fertile branch persists and the other branch may disappear. In the vegetative phase, on the other hand, the fertile branch may be suppressed and the leaves alone may persist. Androphyll, gynophyll and togophyll (sterile) together form gonophyll. Flower on the other hand becomes a compound inflorescence. But the anatomical studies do not support this idea.

Placentation

In the past there has been a controversy around whether the ovules are carpellary, axial or both as regard to their attachment. According to classical concept of carpel are borne on the carpellary margins. However there are examples where ovules are attached on the tip of the axis *eg*. In *Ochna* it is observed that the vascular of the axis directly supply the ovule (Govil and Upendra 2010) .According to the classical concept each placenta is a double structure, each half being contributed by a carpellary margin. This duality is clear in the transverse sections of flower (i) two halves are separated by a groove (ii)The two ventral bundles of a carpel remain more or less remain distinct,(III) the orientation ovules is in opposite direction. Puri (1951) has given criteria of assigning the different type of placenta. For details see Puri (1952).

Inferior ovary

The problem of nature of outer wall of inferior ovary is another controversy related with flower. The main problem lies in whether it is axial in nature or axial in nature. Puri (1952) has suggested that the nature of ovary depends upon the position of intercalary meristem formed, if it is formed just at the base of sepal, petal and stamens the inferior ovary will be appendicular, if in the region of cortex, it will be partly appendicular and partly axial and if inside the vascular supply then it will be axial in nature (Puri 1952)

The morphology of flower, placentation and inferior ovary are best explained in terms of classical concept which serves as most accepted solution.

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